Received: 25 June 2020 | Revised: 8 March 2021 | Accepted: 11 June 2021

DOI: 10.1002/aqc.3672

RESEARCH ARTICLE

WILEY

Preliminary evidence of an endangered species benefiting from moderate climate warming: A palaeolimnological study of the charophyte *Lychnothamnus barbatus*

Michał Brzozowski[1] | Grzegorz Kowalewski[2] | Witold Szczuciński[3] | Lech Kaczmarek[4] | Mariusz Pełechaty[1]

[1]Department of Hydrobiology, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland

[2]Department of Biogeography and Paleoecology, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Poznań, Poland

[3]Geohazards Research Unit, Institute of Geology, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Poznań, Poland

[4]Ecological Station in Jeziory, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland

Correspondence
Michał Brzozowski and Mariusz Pełechaty, Adam Mickiewicz University, Poznań, Faculty of Biology, Department of Hydrobiology, ul. Uniwersytetu Poznańskiego 6, 61-614, Poznań, Poland.
Email: michal.b@amu.edu.pl; mbrzozowsk@gmail.com; marpel@amu.edu.pl

Funding information
Ministerstwo Nauki i Szkolnictwa Wyższego (Polish Ministry of Science and Higher Education), Grant/Award Number: Diamond Grant no. DI2015017045

Abstract

1. In a time of rapid environmental changes, identification of the effects of climate warming on charophytes (Characeae, Charophyta) will enable the optimization of conservation measures, especially for extremely rare species. *Lychnothamnus barbatus* is one of the rarest charophytes worldwide, which has decreased in the number of occupied sites over the last century. However, the recolonization of former sites has been observed in recent years (e.g. Lake Kuźnickie, Poland). The study aimed to analyse the effects of climatic changes and human pressure on the *L. barbatus* population.
2. Three 30 cm sediment cores were collected from minimum, average, and maximum depths of *L. barbatus* occurrence to determine the past vegetation composition. Sediment cores were dated using the radioisotopes lead-210, caesium-137, and carbon-14. A spatial analysis of the lake catchment changes during the last 120 years was also conducted.
3. The study demonstrated *L. barbatus* presence in Lake Kuźnickie at the beginning of the 16th century. However, a sharp increase in the proportion of this species in the vegetation community occurred in the 19th century and during climate warming at the end of the Little Ice Age. Factors that significantly influenced the present occurrence of the *L. barbatus* population included improvement in water quality and the oospore bank deposited in the bottom sediments.
4. This study is the first palaeoreconstruction in a modern lake dominated by *L. barbatus*. Based on the history of *L. barbatus* in Lake Kuźnickie after the end of the Little Ice Age, the positive effect of climate warming on the contemporary recovery of this charophyte is postulated.
5. The reaction of *L. barbatus* to climate warming appears to differ from commonly accepted scenarios for aquatic macrophytes because its recovery in the past and at present coincided with increases in air temperature. This research indicated the appropriate management and conservation practices for lakes with *L. barbatus* populations.

KEYWORDS
climate change, conservation/biodiversity, freshwaters, Late Holocene, palaeolimnology

1 | INTRODUCTION

Charophytes (stoneworts, Charophyta) are macroscopic green algae, currently represented by six genera worldwide (*Chara*, *Nitellopsis*, *Lychnothamnus*, *Lamprothamnium*, *Nitella*, and *Tolypella*). As a group, charophytes are found in the waters of all continents but occur mainly in low-fertility fresh waters (Schubert et al., 2018). Remains of stoneworts are frequently well preserved in bottom sediments. Thus, charophyte fossils are used as a proxy for nutrient-poor aquatic environments to reconstruct the palaeoenvironment (Soulié-Märsche & García, 2015; Kowalewski et al., 2016).

Despite their worldwide distribution, charophytes are becoming increasingly rare and endangered components of aquatic ecosystems. There are a few antagonists of stoneworts in the environment, including competitively stronger higher plants in areas with increased water fertility (Blindow, Hargeby & Hilt, 2014) and increased human activity, which causes the loss of charophyte species and their habitats. When light is not a limiting factor, *Chara* species can maintain high growth rates even at elevated phosphorus concentrations (Blindow, 1988). Thus, water eutrophication (increasing nutrient concentration and phytoplankton biomass) and low light availability usually restrict charophyte occurrence to shallow sites (Blindow, 1992). This withdrawal of charophytes to shallower littoral regions, where they must compete with vascular vegetation, often leads to their disappearance from water bodies (Blindow, 1992; Van den Berg et al., 1999). Classical succession theory suggests that whereas stoneworts are early or 'pioneer' components of aquatic vegetation (Stewart & Church, 1992), they are replaced by angiosperms and phytoplankton when the nutrient concentration and turbidity increase (Blindow, 1992). However, in recent years, the co-occurrence of charophytes with vascular plants has been increasingly observed, including bioindicators of eutrophic waters (e.g. the rigid hornwort *Ceratophyllum demersum* L.; Pełechaty, Pronin & Pukacz, 2014; Brzozowski, Pełechaty & Pietruczuk, 2018). Moreover, charophyte renewal at the expense of vascular vegetation has also been reported under conditions of lake re-oligotrophication and increased light availability (Richter & Gross, 2013).

Charophytes can renew their populations in two ways: vegetative propagation and, generatively, via oospores (Skurzyński & Bociąg, 2011; Beilby & Casanova, 2014). After oospore calcification, gyrogonites are produced by some charophyte species (Soulié-Märsche & García, 2015). Gyrogonites are the parts of charophytes that are well preserved in sediments and sedimentary rocks. Along with oospores, they are commonly applied in palaeoreconstructions as bioindicators of low-water trophic status and differing salinity levels (Martín-Closas, Wójcicki & Fonollá, 2006; Rodrigo, Alonso-Guillén & Soulié-Märsche, 2010).

At present, little is known about the concomitant effects on charophytes of global warming and other large-scale environmental perturbations (Pełechata, Pełechaty & Pukacz, 2015; Rojo et al., 2017). According to the Intergovernmental Panel on Climate Change (2013), the global average temperature will increase between 0.3°C and 6.4°C by the end of this century. This may have profound effects on biodiversity and ecosystem functioning of fresh waters, particularly lakes (Moss et al., 2009; Dziuba et al., 2020), including the growth of charophytes (Puche et al., 2018). Some of the charophyte species will react negatively, whereas other species may potentially be global warming beneficiaries (Auderset Joye & Rey-Boissezon, 2015; Sleith, Wehr & Karol, 2018; Choudhury et al., 2019). Therefore, it is essential to determine which charophyte species will benefit from the observed climatic changes, whether common or rare. Identification of climate change effects on charophytes will enable the optimization of conservation measures for this valuable group of macrophytes, especially extremely rare species.

One of the rarest charophyte species worldwide is *Lychnothamnus barbatus*, the macroalga characterized by a disjunctive, Euro-Australasian distribution (Casanova, García & Feist, 2003; Bhatia, 2006; Sugier et al., 2010). The species is threatened by extinction, and is Red-listed in Poland (Siemińska et al., 2006), Lithuania (Sinkevičienė, 2010), Germany (Schnittler & Ludwig, 1996), the Balkans (Blaženčić et al., 2006), and Australia, where the species was the first endangered non-vascular plant (Bostock & Holland, 2010). In Poland, *L. barbatus* is under strict protection because, in the *Red List of Plants and Fungi in Poland* (Mirek et al., 2006), it is classified as an endangered species of algae (Siemińska et al., 2006). However, it has recently been suggested that this species (Figure 1) should be considered critically endangered according to categories of the International Union for Conservation of Nature (Urbaniak & Gabka, 2014).

In the second half of the 20th century, the disappearance of *L. barbatus* sites was related to increasing water eutrophication (Sugier et al., 2010; Pełechaty, Brzozowski & Pietruczuk, 2017). At present, there are only 55 sites containing *L. barbatus* (mainly in lakes) worldwide, and from the end of the 19th century, 63 sites have disappeared (Pełechaty, Brzozowski & Pietruczuk, 2017). Surprisingly, in recent years *L. barbatus* has expanded its geographical range to North America (Karol et al., 2017). Furthermore, the processes of recolonization (Raabe et al., 2012; Sinkevičienė & Urbaitė-Maževič, 2012; Pełechaty, Brzozowski & Pietruczuk, 2017) and colonization (Karol et al., 2017) of lakes by *L. barbatus* have been observed. Lake Kuźnickie is one such lake. The recovery of the *L. barbatus* population was documented in 2008 after its disappearance in the late 1980s (Pełechaty, Brzozowski & Pietruczuk, 2017).

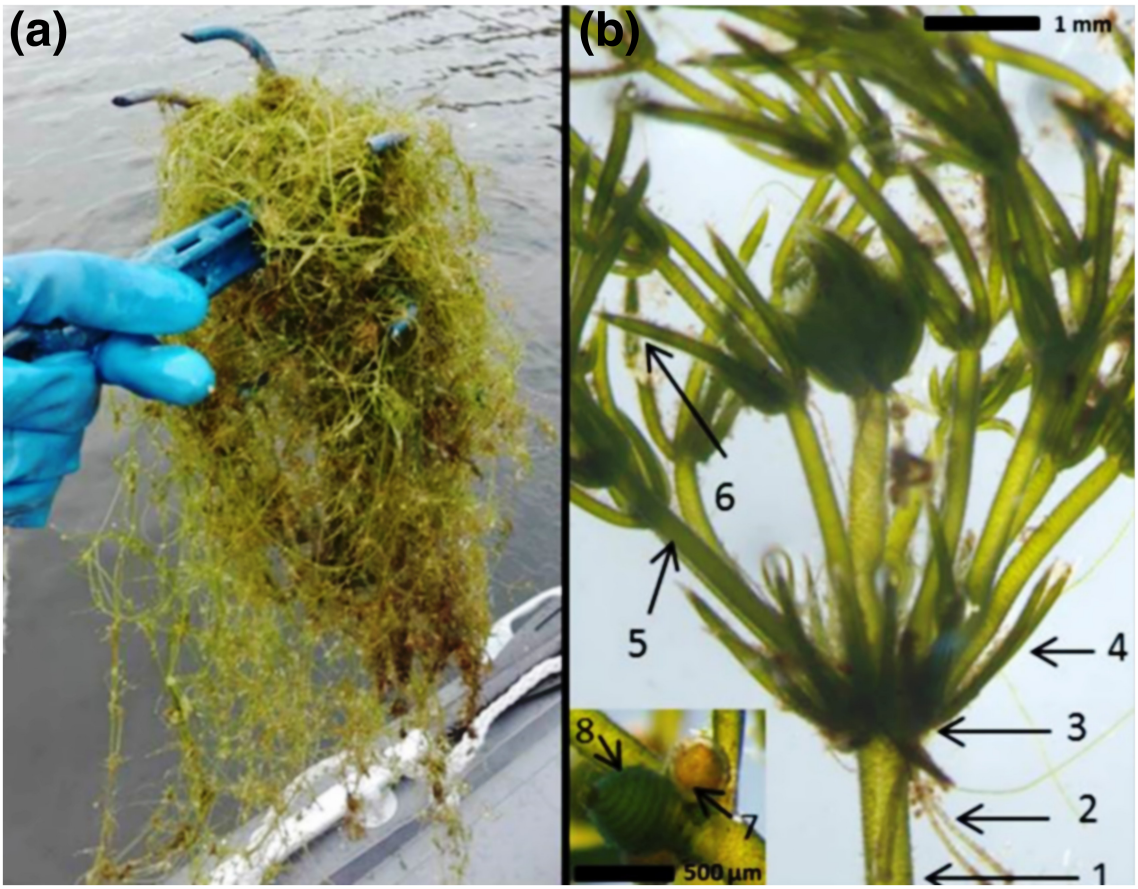

FIGURE 1 (a) *Lychnothamnus barbatus* thalli from Lake Kuźnickie (Wielkopolska region, western Poland). (b) Distinctive features of *L. barbatus* morphology: 1, main axis; 2, cortex cells (incomplete cortication); 3, node; 4, stipulodes; 5, branchlet; 6, bract cell, 7, antheridium; 8, oogonium

Lychnothamnus barbatus is a charophyte capable of wintering in warm conditions (Pełechaty, Brzozowski & Pietruczuk, 2017), which enables the perennial growth of the species in Lake Kuźnickie and its increased distribution in the littoral zone (Brzozowski, Pełechaty & Pietruczuk, 2018). The known ecological preferences of *L. barbatus*, combined with increasingly observed milder winters with short durations of lake-ice cover (Choiński et al., 2015; Czernecki & Ptak, 2018; Bartosiewicz et al., 2020), indicate that global warming may have a significant impact on the recovery of this species in the aquatic ecosystems of temperate climatic zones. Based on the literature (Raabe et al., 2012; Sinkevičienė & Urbaitė-Maževič, 2012; Karol et al., 2017) and our observations (Pełechaty, Brzozowski & Pietruczuk, 2017), a research hypothesis was formulated: that environmental changes related to global warming provide a competitive advantage to the endangered and indicatory *L. barbatus*, favouring its spread and expansion in the littoral regions of lakes in temperate climatic zones. The present study was conducted in Lake Kuźnickie that currently hosts one of the most abundant and well-developed populations of *L. barbatus* (Brzozowski et al., 2019; Brzozowski et al., 2021). The hypothesis was verified by reconstructing the history of *L. barbatus* in this model lake by applying an analysis of macroremains in the dated lake sediment cores in the context of climate and lake catchment changes. Moreover, based on this research, the most crucial management and conservation practices for *Chara* lakes, especially with abundant *L. barbatus*, are discussed.

2 | METHODS

2.1 | Study lake

The study was performed in Lake Kuźnickie (52°12′56.7″N, 16°05′31.0″E), a dimictic and fully stratified water body located in the north-western area of the Poznań Lake District (western Poland; Pełechaty, Brzozowski & Pietruczuk, 2017). The lake is 75.7 ha, and the maximum and mean depths are 13.2 m and 7 m respectively (Radziej, 1959). At present, Lake Kuźnickie does not have any outflows or inflows. In the past, on the western shore of the lake, a drainage ditch was created in the second half of the 19th century, which acted as an outflow; thus, the lake is currently fed by groundwater and precipitation. A relatively low mean annual precipitation of 513 mm varies within 344–815 mm (Woś, 1994). The highest precipitation occurs in July (73 mm), whereas the lowest (25 mm) occurs in February and March. Mean temperatures below zero occur between December and March, and the average winter

temperature is −0.9°C. The mean annual temperature is 8.0°C (Woś, 1994). The lake is used for recreational purposes and is managed by the Polish Angling Association (Polski Związek Wędkarski). Arable fields and rural areas are limited to a zone adjacent to the western shore of the lake, whereas forests predominate in the remaining part of the catchment.

Lychnothamnus barbatus was found in Lake Kuźnickie in 1978 (Gołdyn, 1983), but the species declined at the beginning of the 1980s (Gołdyn, personal communication, 2016; Pełechaty, Brzozowski & Pietruczuk, 2017). In 2008, *L. barbatus* was rediscovered in Lake Kuźnickie by the Voivodship Inspectorate of Environment Protection in Poznań during a monitoring study (Pełechaty, Brzozowski & Pietruczuk, 2017). Currently, *L. barbatus* is one of the dominant species in the submerged vegetation community. Other co-dominants are the two vascular plants *Ceratophyllum demersum* L. and *Myriophyllum spicatum* L. and the cosmopolitan charophyte *Nitellopsis obtusa* (N.A. Desvaux) J. Groves. The lake water quality has improved in recent years, with the lake now classified as mesotrophic (Brzozowski & Pełechaty, 2020; Brzozowski et al., 2021).

2.2 | Sampling of sediment cores and the determination of macroremains

Three 30 cm long sediment cores were collected along a transect in the central-western littoral part of Lake Kuźnickie using a gravity corer (UWITEC GmbH, Mondsee, Austria) equipped with an 86 mm inner diameter tube. The cores were taken from depths of the occurrence of *L. barbatus* along transect T1: a minimum of 2 m (K1 site), a maximum of 5 m (K3 site), and an average of 4 m (K2 site) (Brzozowski et al., 2019).

From the K1 and K2 sites, two parallel cores were collected to determine the age of the sediments (K1-A and K2-A) and to analyse the content of macroremains (K1-B and K2-B), whereas a single core from site K3 was used for both types of analysis. The cores were subsampled with a 1 cm resolution and stored at 4°C.

During analysis, 1 cm thick subsamples of 30–50 cm^3 were washed through a 0.125 mm mesh sieve. The residue was examined under a stereomicroscope (Nikon, Tokyo, Japan) at 10–100× magnification using a Bogorov counting tray. Recognizable plant and animal fossils were isolated, identified, and counted. Charophyte fructifications, the oospores and gyrogonites (calcified oospores), were classified into one category, hereafter the oospores. All plant and invertebrate macroremains, excluding those documented by presence–absence (mostly impermanent vegetative plant fragments), were expressed in numbers per 100 cm^3 of fresh sediment. Stratigraphic diagrams were plotted using the R rioja package v. 15.1 (Juggins, 2017). Macroremains were subjected to stratigraphically constrained cluster analysis to determine zones. After standardization, stratigraphic zones were identified using Gower distance (Legendre & Legendre, 1998; Birks, 2014) and the CONISS method (Grimm, 1987). The optimum number of zones in each sediment profile was determined using the 'broken-stick' model (Bennett, 1996).

To illustrate the underlying patterns in the analysed core composition and macroremain structure, nonmetric multidimensional scaling (NMDS) was applied. This multivariate technique for unconstrained ordination effectively extracts underlying gradients in community composition (Kruskal, 1964). Along with NMDS, an analysis of similarities (ANOSIM) was performed to test the statistical significance of differences between two or more groups of stratigraphic zones (Oksanen, 2010). The tested hypothesis stated that differences between groups were significant.

2.3 | Dating of sediment cores

The sediment samples were weighed using a laboratory scale (RADWAG AS60/220/C/2, Radom, Poland) with 0.001 g measurement precision. The samples were dried to a constant weight using an SLW 115 laboratory dryer (POL-EKO-APARATURA, Wodzisław Śląski, Poland). The entire sediment sample was powdered and combusted at 550°C for 4 h and subsequently at 925°C for 2 h (Heiri, Lotter & Lemcke, 2001). The weight loss on ignition at 550°C was presumed to represent the percentage of organic matter (OM). The carbonate (CO_3^{2-}) content was calculated by multiplying the mass of carbon dioxide evolved in the second step of the analysis by 1.36. Finally, the calcium carbonate ($CaCO_3$) content was calculated by multiplying the CO_3^{2-} content by 1.66. Based on the OM and CO_3^{2-} contents, sediment samples derived from parallel cores (sediment dating: K1-A and K2-A cores; determination of macroremains: K1-A and K1-B cores) were correlated. Spearman rank correlation was applied because the data distribution of both variables was inconsistent with the theoretical normal distribution (Shapiro–Wilk test). The parallel cores studied were highly correlated (Figure 2).

The dating of sediments was based on the combination of the caesium-137 (^{137}Cs), lead-210 (^{210}Pb), and carbon-14 (^{14}C) methods. Activities of ^{137}Cs, ^{210}Pb, lead-214, and bismuth-214 used to assess supported ^{210}Pb were measured using a Canberra BE3830 gamma spectrometer (Mirion Technologies, Inc., San Ramon, California, USA) with a remote detector chamber (6 in.) for low-energy background reduction. The efficiencies for the sample geometries were determined using the Laboratory Sourceless Calibration Software (LabSOCS; Mirion Technologies, Inc., San Ramon, California, USA) code, which applies all corrections for sample geometry, matrix, and container type. The activity of excess (ex) ^{210}Pb was obtained from the difference between total ^{210}Pb activity and supported ^{210}Pb activity. Samples 1 cm thick were dried, ground, and packed into sealed containers for further analyses (lasting up to several days), which took place several weeks later. The sediment accumulation rate (SAR), and thus the estimated age–depth relationship, was based on the identification of the ^{137}Cs maxima. This corresponds to the atmospheric nuclear bomb testing before the Nuclear Test Ban Treaty in 1963, a peak related to the Chernobyl accident from 1986, and the likely near-surface peak related to the 2011 accident in Fukushima. For the past 100 years, the SAR was also assessed based on ex ^{210}Pb.

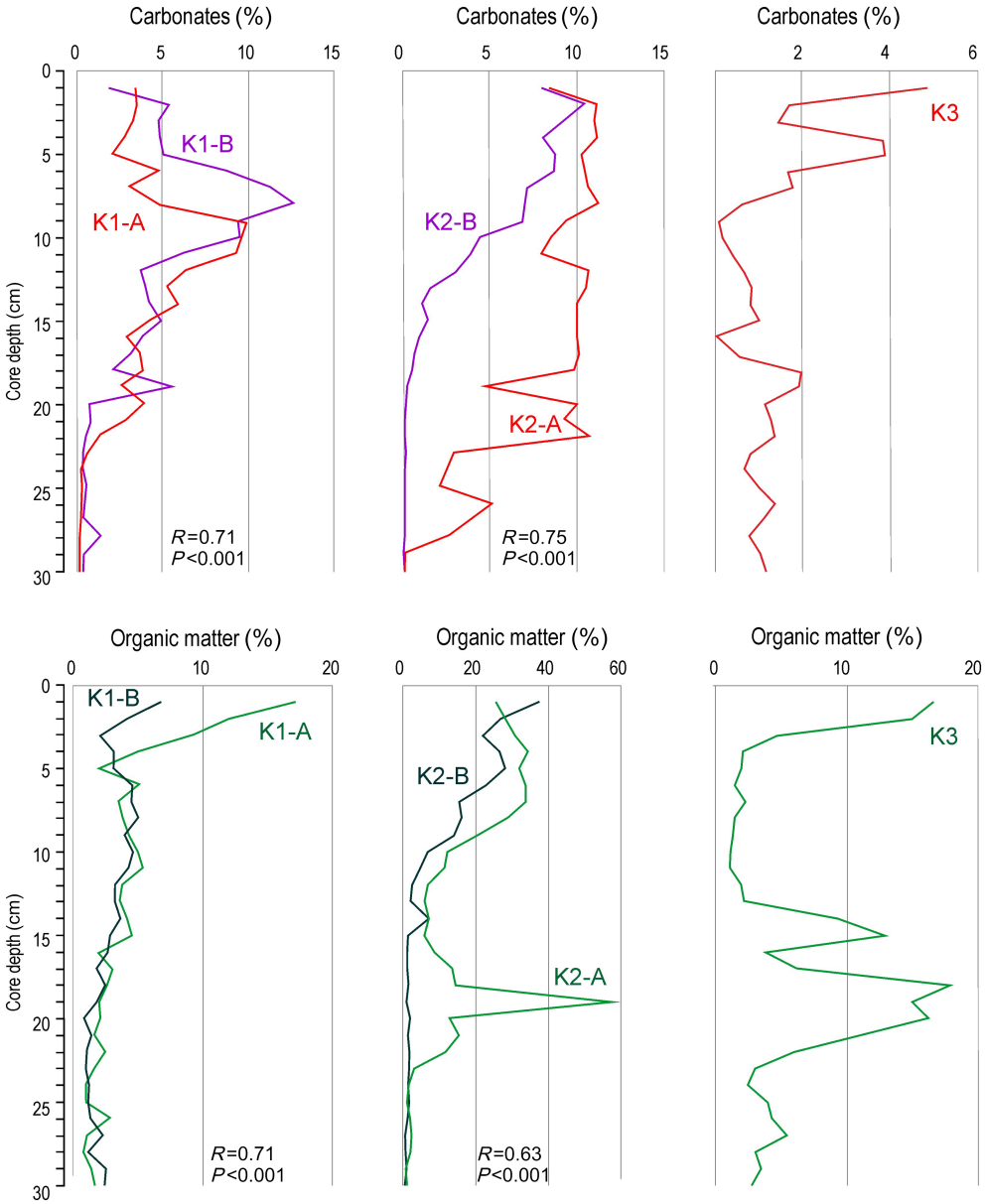

FIGURE 2 Carbonate and organic matter content in sediment cores collected from the minimum depth (K1-A, sediment dating; K1-B, analysis of macroremains), average depth (K2-A, sediment dating; K2-B, analysis of macroremains), and maximum depth (K3) of *Lychnothamnus barbatus* occurrence in Lake Kuźnickie. Sediment samples derived from parallel cores (K1-A and K1-B; K2-A and K2-B) were correlated (Spearman rank correlation, *R*; significance level, *P*) using the organic matter and carbonate content

Among several available models, the constant initial concentration model (Robbins & Edgington, 1975; McKee, Nittrouer & DeMaster, 1983) provided the best agreement with ^{137}Cs dating and was applied in this study.

Three terrestrial plant remains taken from the lowermost samples of each core were radiocarbon (^{14}C) dated using accelerator mass spectrometry by Beta Analytic Inc. (Miami, Florida, USA). The same samples were also analysed for the ratio of stable isotopes carbon-13: carbon-12 (δ^{13}C). The radiocarbon results were converted into calendar years using the highest probability density range method (Bronk Ramsey, 2009) and the IntCal13 calibration curve (Reimer et al., 2013).

2.4 | Analysis of catchment changes

The reconstruction of changes in the catchment area of Lake Kuźnickie was made using available historical topographic maps from 1896, 1940 (Archive of Maps of Western Poland, http://mapy.amzp.pl/), 1977, and 1990 (Provincial Center for Geodesic and Cartographic Documentation, WODGiK; Wojewódzki Ośrodek Dokumentacji Geodezyjnej i Kartograficznej). The Forest Data Bank (https://www.bdl.lasy.gov.pl/portal/en) was used to retrieve data for 2017 and gain information on the species structure and age of the forests. Using the QGIS Lyon software (https://qgis.org/en/site/), the land cover was categorized into four classes: wetlands, deciduous forest, coniferous forest, and farmlands. Their percentage share was determined for the years 1896, 1940, 1977, 1990, and 2017.

2.5 | Analysis of meteorological data

To determine changes in air temperatures and precipitation, the available data for the last 70 years (1951–2018) from the nearest station of the Institute of Meteorology and Water Management

(Instytut Meteorologii i Gospodarki Wodnej, Wielichowo, station code 252160230) were analysed. The annual and winter mean air temperatures, number of days with temperatures below 0°C, and total annual precipitation were calculated. The Shapiro–Wilk test showed that the meteorological parameters studied were characterized by a consistent or approximate data distribution with the theoretical normal distribution. Therefore, the trends of meteorological factors' changes over time were determined using the Pearson correlation.

3 | RESULTS

3.1 | Climate changes

Based on local meteorological observations, a statistically significant warming trend was observed in the period 1951–2018 (Figure 3). The highest annual mean air temperature reached 10.39°C in 2018, whereas the lowest was 6.66°C in 1956. The annual total precipitation exhibited substantial variability between the highest annual precipitation of 812.6 mm in 1967 and the lowest precipitation of 329.8 mm in 1982 (Figure 2). The mean winter temperature over the last 70 years was 0°C, whereas the lowest (−7°C) and the highest (4°C) mean winter temperatures were in 1954 and 2007 respectively (Figure 3). In the period analysed, increases in mean winter temperature and annual total precipitation were observed (Figure 3). In addition, the number of days with a temperature below 0°C decreased slightly over the same period (Figure 3), but this tendency was not statistically significant.

3.2 | Changes in the catchment land-cover structure of Lake Kuźnickie

The catchment basin, excluding the lake, has a surface area of 200.3 ha. The land cover has not changed significantly since 1896 and is dominated by more than 80% of coniferous forest (Table 1). Pines dominated in the tree stand, whereas alders dominated in the coastal lake zone. Larch and birch constituted a negligible proportion. More than 37% of the tree stand is older than 90 years, indicating high stability of forest vegetation. Deciduous forest cover revealed a slightly increasing tendency in the late 1970s and stabilized while the proportion of wetlands decreased. Agricultural areas did not change significantly during the study period (Table 1).

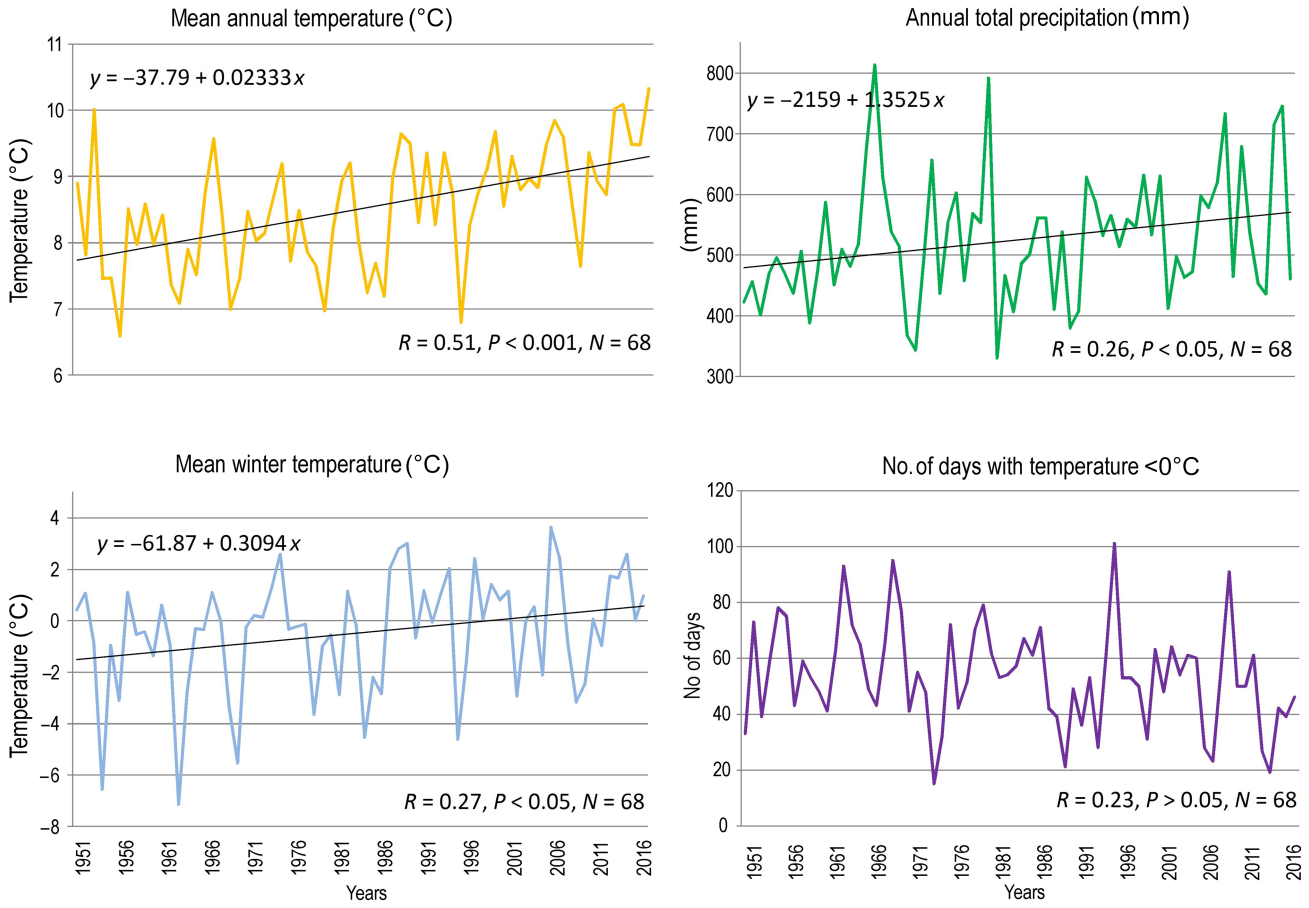

FIGURE 3 Annual and winter mean air temperature (December, January, and February), total precipitation, and number of days with daily mean temperature below 0°C at Wielichowo meteorological station, located ca. 20 km eastwards from Lake Kuźnickie. Data from the Institute of Meteorology and Water Management–National Research Institute have been processed

3.3 | Sedimentation rate and age of sediment cores

^{137}Cs was present at low levels throughout the K1 core (Figure 4). However, in the lower parts, its activity was minimal and probably caused by downward mixing processes. Based on the identification of assumed ^{137}Cs peaks, the present SARs are approximately 0.25 cm year^{-1} to 0.39 cm year^{-1}. The ex ^{210}Pb showed a steady decrease with depth. The calculated SAR was approximately 0.12 cm year^{-1}, and its depth range was limited to <25 cm, suggesting that deeper sediments are older than 100–120 years. The radiocarbon date from the deepest sample was older than 3000 years (Table 2) and is likely to have come from redeposited plant remains. Thus, considering all the available evidence, the deepest samples in the core are likely to be 250 years old or younger. Moreover, some sediment mixing and redeposition have occurred.

In core K2, the ^{137}Cs activities were limited mainly to the upper ca. 10 cm and presented a relatively uniform profile, whereas some low activity was detected down to 18 cm (Figure 4) and were likely caused by mixing. The recent ^{137}Cs-based SAR was ca. 0.14 cm year^{-1}. The ex ^{210}Pb profile (Figure 4) suggested a relatively high accumulation rate for the upper ca. 8 cm of the sediment core in the order of 0.2 cm year^{-1}, and lower ones down to

TABLE 1 Changes in the land cover of the Lake Kuźnickie catchment area since the end of the 19th century

		Forest (%)		
Year	Wetlands (%)	Deciduous	Coniferous	Farmland (%)
1896	7.33	8.96	81.96	1.75
1940	7.03	9.03	81.79	2.14
1977	1.26	16.11	80.87	1.76
1990	1.11	13.87	82.83	2.19
2017	2.69	14.25	81.07	1.99

Note: Data presented as percentage of the catchment area.

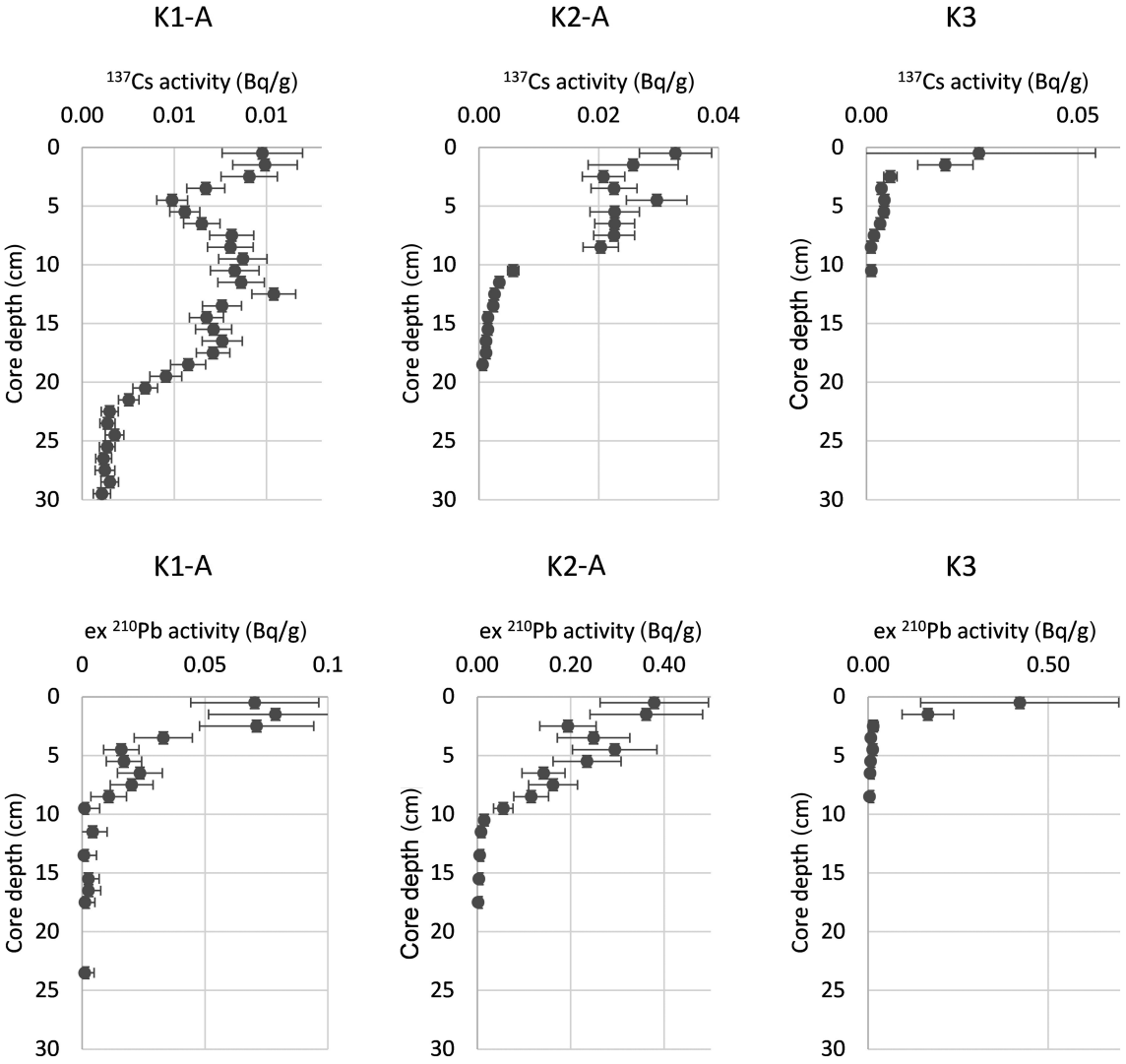

FIGURE 4 The downcore changes in caesium-137 (^{137}Cs) and excess lead-210 (ex ^{210}Pb) activities. The vertical bars refer to the sediment sample thickness (1 cm) analysed, whereas horizontal bars refer to two sigma uncertainty

TABLE 2 Accelerator mass spectrometry (AMS) carbon-14 (^{14}C) dates, calibrated dates, and ratio of stable isotopes carbon-13:carbon-12 ($\delta^{13}C$) values of the samples from the cores investigated

Core no.	Depth (cm)	Material	Lab no.	Raw AMS ^{14}C BP	Calibrated years BP ± 2σ	$\delta^{13}C$ (‰)
K1	30	Plant remains	Beta—491840	3,070 ± 30	(94.7%) 3,364–3,209	−26.8
					(0.7%) 3,189–3,185	
K2	30	Plant remains	Beta—491841	120 ± 30	(62.8%) 150–10	−27.4
					(32.6%) 272–186	
K3	30	Plant remains	Beta—491842	1,020 ± 30	(90.3%) 982–904	−29.3
					(4.1%) 856–830	
					(0.7%) 809–803	
					(0.3%) 1,042–1,038	

Note: Calibration with BetaCal3.21, using highest probability density range method (Bronk Ramsey, 2009) and IntCal13 calibration curve (Reimer et al., 2013).

12 cm in the order of ca. 0.03 cm year^{-1}. However, the rapid decline in ^{137}Cs and ex ^{210}Pb activities at approximately 10 cm depth coincides with changes in sediment properties reflected by geochemical properties (Figure 3), suggesting a hiatus or essential change in sedimentation conditions. In the case of a hiatus, the ^{137}Cs-based accumulation rate must be treated as the minimum value, and the recent accumulation is likely to be approximately 0.2 cm year^{-1}. Applying this rate to the total length of the core, the bottom samples would be approximately 150 years old. The age would be in the range of the calibrated ^{14}C dating of the sample from the deepest part of the core. However, this assessment must be interpreted with caution, and possible changes in sedimentation conditions and compaction should be considered, as well as the relatively large calibration ranges for ^{14}C dating (1680–940) in the core bottom sample.

In core K3 (Figure 4), elevated activities of ^{137}Cs and ex ^{210}Pb were present only in the upper 2–3 cm, whereas very low activities were present down to ca. 10 cm of sediment depth probably caused by downward mixing. The calculated SARs for the youngest sediments were in the order of 0.03 cm year^{-1} and 0.02 cm year^{-1} using ^{137}Cs and ex ^{210}Pb respectively. Applying these rates to the whole core, the sediment core bottom would be approximately 1,000–1,500 years old. The younger age agrees with the calibrated ^{14}C age of the core bottom sample.

3.4 | Evidence of temporal changes in the abundance of *Lychnothamnus barbatus*

Analysis of macroremains resulted in identifying submerged macrophytes, telmatic plants, trees, and aquatic invertebrates. Variability in their proportion, as well as lithological and geochemical changes in the sediments, allowed the identification of several zones (units) along the cores, which are described in chronological order from the oldest (bottom of the sediment cores) to the youngest (surface sediments).

3.4.1 | The shallow phytolittoral core K1

The lithological changes, as well as the composition of organic macroremains, allowed the division of this core into three main sections (Figure 5): zones K1-1, K1-2, and K1-3, covering sediment depths of 30–19 cm, 18–6 cm, and 5–1 cm respectively. The deepest zone (K1-1) is subdivided into two subzones (K1-1a, 30–22 cm, and K1-1b, 21–19 cm).

The K1-1 zones are characterized by gravel and the common occurrence of fine sand and by relatively low contents of OM and CO_3^{2-}. In the K1-1a subzone, two groups of macrofossils were distinguished: (i) the remains present only in this subzone; that is, undetermined peat-like remains and Turbellaria cocoons; and (ii) remains present also in the overlying layers, but in small amounts (Figure 5). The proportion of *L. barbatus* macroremains was minor in this subzone. In the K1-1b subzone, the total number of plant remains was small; however, compared with that of the lower zone, a higher proportion of *L. barbatus* oospores and other charophytes was observed (Figure 5).

In zone K1-2, OM contributions and CO_3^{2-} generally increased upwards (Figure 5). Fossils of macrophytes were the most diverse in this zone, including oospores of *L. barbatus*, *Chara* sp., and macroremains of submerged angiosperms (Figure 5). Zone K1-2 was characterized by numerous colonies of *Gloeotrichia* sp., reaching their maximum frequency. Aquatic invertebrate remains, fishbone fragments, the remains of trees, and *Juncus* sp. seeds were also numerous.

Zone K1-3 exhibited a slight increase in OM content, whereas the CO_3^{2-} content was relatively low. *Lychnothamnus barbatus* and *Chara* sp. remained at their maximum frequencies in this zone, with a dominance of *L. barbatus* (Figure 5). Among angiosperms, seeds of *Myriophyllum* sp. appeared for the first time (Figure 5). The remains of invertebrates, mainly Cladocera, were numerous, but the number of fish remains and their parasites decreased compared with that in zone K1-2.

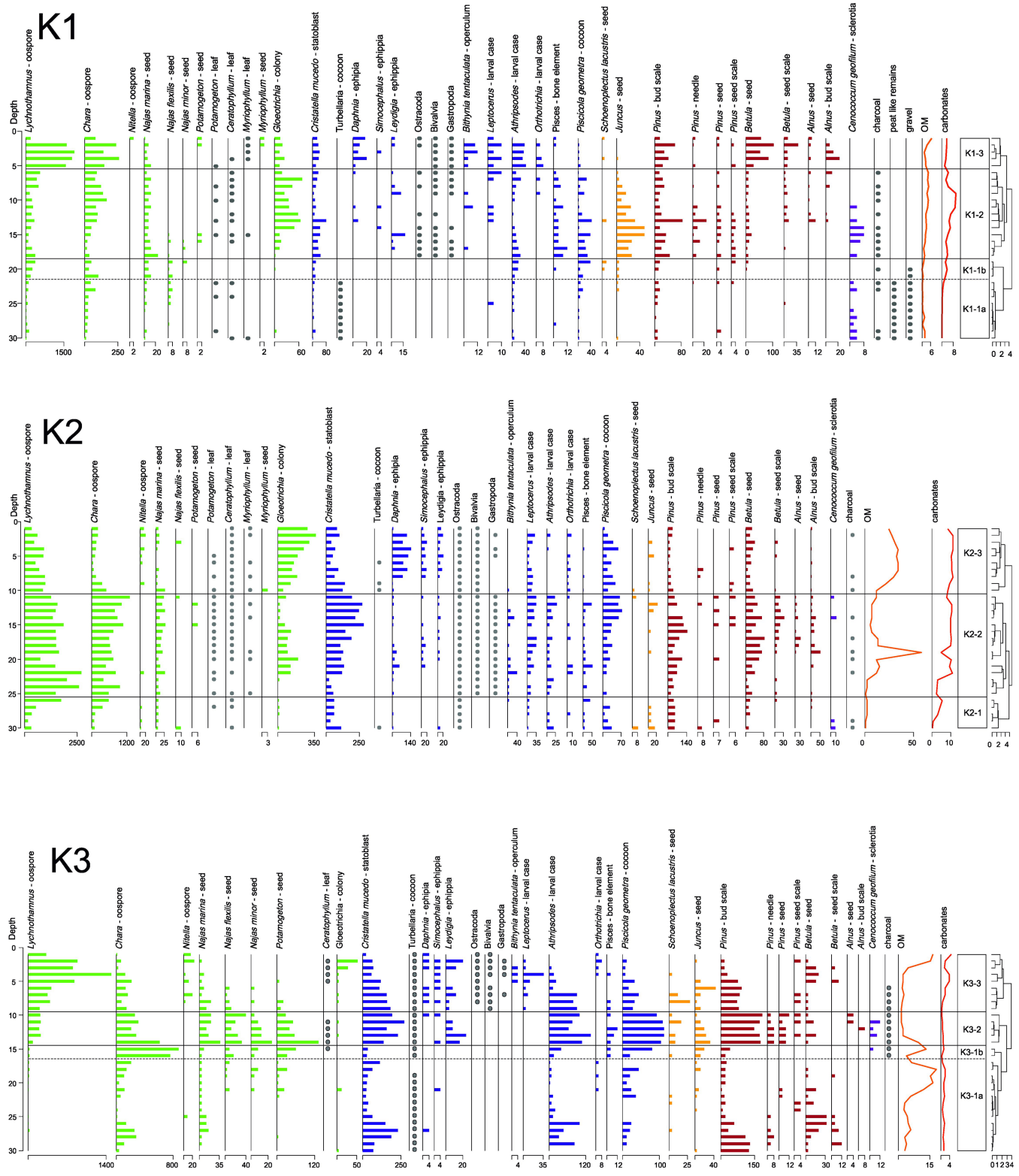

FIGURE 5 Changes in frequencies of macroremains and geochemical properties in the cores studied and cluster analysis of macroremains to determine stratigraphically constrained zones. Green bars, submerged aquatic vegetation and algae; dark violet bars, aquatic animals; orange bars, costal vegetation; red bars, trees; lighter violet, fungus *Cenococcum geophilum*; grey circles, occurrence of taxon

3.4.2 | The intermediate-depth phytolittoral core K2

This core was divided into three zones (Figure 5): K2-1, K2-2, and K2-3, spanning sediment depths of 30–26, 25–11, and 10–1 cm respectively.

The K2-1 zone was characterized by low OM and CO_3^{2-} content. Oospores of *L. barbatus* and *Chara* sp. were present in each sample and showed an upward increasing trend with a low proportion of angiosperm remains. Among the invertebrates, statoblasts of *Cristatella mucedo* were common, as were the remains of caddisflies and *Piscicola geometra*. Shells of Ostracoda occurred in the same amounts throughout the entire core.

Zone K2-2 was characterized by an increase in CO_3^{2-} and OM content, except for a single sample, where OM reached a maximum unique value of more than 57% (Figure 5). Oospores of charophytes reached their maximum in this zone, particularly *L. barbatus*. Macroremains of aquatic plants were represented mainly by *N. marina*, followed by *Ceratophyllum* sp., *Potamogeton* sp., and *Myriophyllum* sp. The remains of *Gloeotrichia* sp., *P. geometra*, and caddisflies were frequent, as were *C. mucedo* statoblasts with the most frequent occurrence in this zone.

The K2-3 zone significantly differed from the lower zone. The OM content reached its highest values (Figure 5), whereas $CaCO_3$ content remained stable. The number of oospores of *L. barbatus* and *Chara* sp., as well as the seeds of *N. marina*, declined sharply. The vegetative remains of vascular macrophytes were still present. The number of colonies of *Gloeotrichia* sp. increased upward. Ephippia of Cladocera were highly abundant, especially those of *Daphnia* sp.; however, the number of *C. mucedo* statoblasts and the number of caddisflies decreased (Figure 5).

3.4.3 | The deep phytolittoral core K3

The deepest core, K3, was divided into three zones: K3-1 (30–15 cm), K3-2 (14–10 cm), and K3-3 (9–1 cm). The lowest zone was subdivided into K3-1a and K3-1b subzones, covering depth ranges of 30–17 and 16–15 cm respectively.

The K3-1a subzone was characterized by high fluctuations in OM content (Figure 5), whereas the proportion of $CaCO_3$ was very low throughout the zone. The contribution of submerged macrophytes was low, except for the oospores of *Chara* sp. in the lower part of the zone. In this subzone, the proportion of *L. barbatus* oospores was negligible. Animal remains were represented by *C. mucedo* statoblasts, followed by *Athripsodes* sp. and a minor proportion of cocoons of *P. geometra* (Figure 5).

The K3-1b subzone had low OM and $CaCO_3$ content. The number of macroremains of submerged macrophytes increased, especially those of *Chara* sp. and *Potamogeton* sp., whereas the proportion of *L. barbatus* oospores was remarkably marginal in this subzone. Invertebrate remains were numerous (Figure 5).

A decrease in OM content characterized the K3-2 zone, and $CaCO_3$ content was very low. Macroremains of submerged macrophytes reached maximum values in the entire core. The number of oospores in *Chara* sp. decreased upward, but the oospores of *L. barbatus* were relatively common (Figure 5). *Cristatella mucedo*, *Athripsodes* sp., and *P. geometra* remained at their maximum values in this zone.

The K3-3 zone was characterized by very low OM content; however, it increased rapidly in the uppermost samples. The amount of $CaCO_3$, although generally not abundant, reached its highest values in the core (Figure 5). The amount of submerged macrophyte macroremains, numerous in the lower zone, decreased significantly upward, except for oospores of *L. barbatus*, which increased sharply (Figure 5). The macroremains of aquatic invertebrates were stable, except for decreasing *C. mucedo*, *P. geometra*, and *Athripsodes* remains.

3.5 | Core composition and stratigraphic zone designation considering NMDS

In the light of NMDS analysis of core K1, the furthest outlying samples were 1 and 11, closer to group K1-3 than its native K1-2 group. The clear emergence of patterns that conformed to constrained groups was supported by ANOSIM (Figure 6). All sedimentary components were significantly correlated with the ordination axes, of which OM exhibited the highest correlation with NMDS1 ($R = -0.95$, $P = 0.001$), followed by mineral matter ($R = 0.91$, $P = 0.001$). CO_3^{2-} content exhibited the highest correlation with NMDS2 ($R = 0.77$, $P = 0.001$). The NMDS results confirmed the main clustering division of the K1 core (Figure 6).

The furthest outlying samples in core K2 were at 29–30 and 10, located on the border of groups, closer to group K2-2 than the native K2-3 group. ANOSIM supported the zone designation ($R = 0.80$, $P = 0.001$) (Figure 6). Mineral sediments primarily influenced the bottom (K2-1) and middle (K2-2) groups (positive value on axis 1), whereas sediments rich in OM and CO_3^{2-} influenced most of the upper group (K2-3). This was in agreement with the major clustering divisions. OM exhibited the highest correlation with NMDS1 ($R = -0.97$, $P = 0.001$), followed by mineral matter ($R = 0.93$, $P = 0.001$). CO_3^{2-} content showed the highest correlation with NMDS2 ($R = -0.74$, $P = 0.001$).

In core K-3, the furthest outlying samples were 1 and 9, related to the K3-2 group rather than their native K3-3 group. The ordination results suggested expanding samples in K2-2 to a range of 9–16, indicating its proximity to subzone K3-1b. The ANOSIM results were $R = 0.68$ and $P = 0.001$ (Figure 6). Sedimentary components revealed a different ordination pattern in core K-3 compared with that of the K1 and K2 cores. Only the proportions of CO_3^{2-} were significantly correlated with the ordination. Some of the variables in this core (e.g. *Chara*, *N. marina*, *C. mucedo*, *Athripsodes*, and OM) revealed a bimodal distribution, indicating

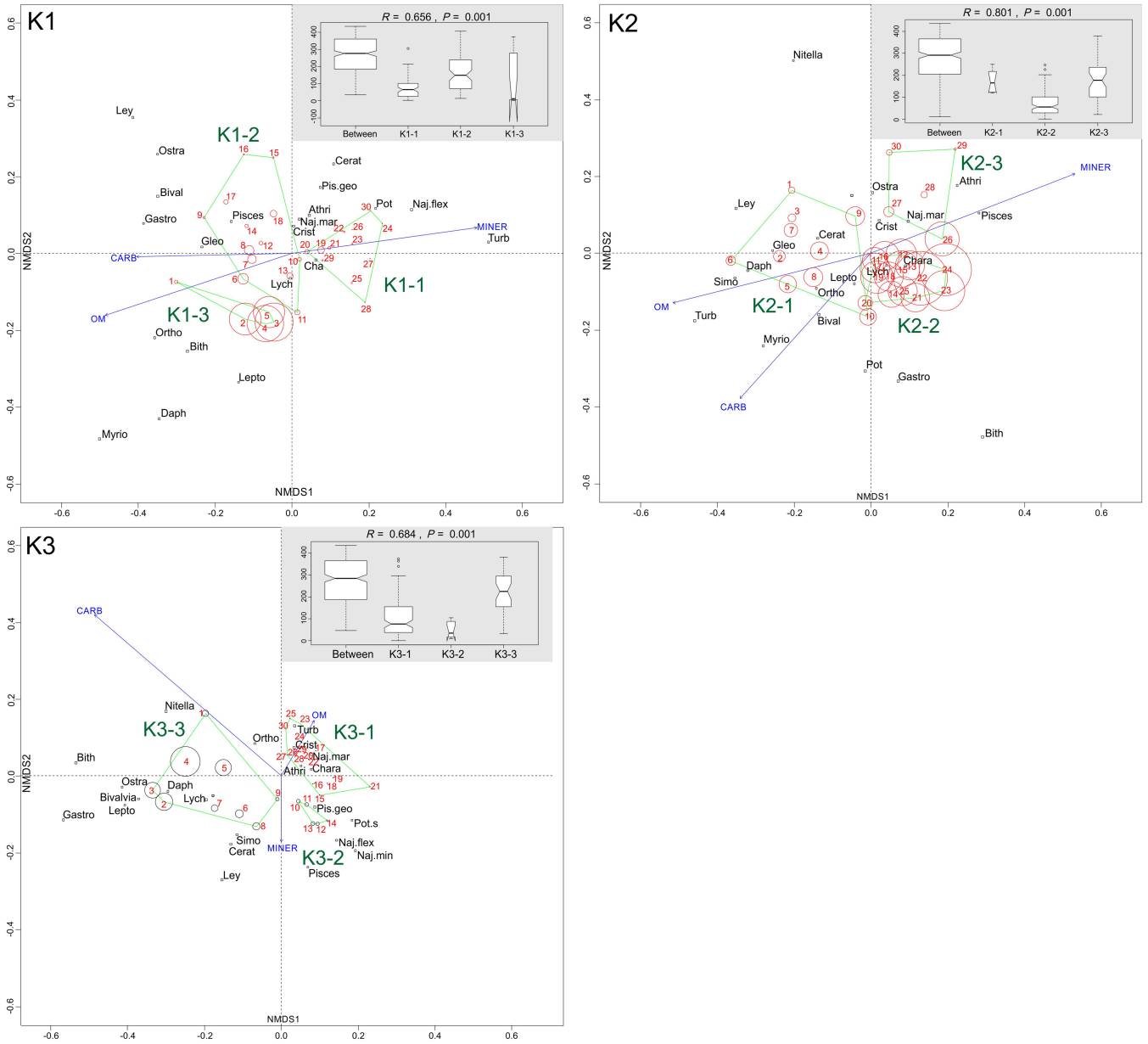

FIGURE 6 Nonmetric multidimensional scaling ordination of macrofossil samples in the cores studied. Analysis of similarities was performed to test statistical differences of zones in sediment cores. Lych, *Lychnothamnus*; Cha, *Chara*; Naj.mar, *Najas marina*; Naj.flex, *Najas flexilis*; Pot, *Potamogeton*; Cerat, *Ceratophyllum*; Myrio, *Myriophyllum*; Gleo, *Gloeotrichia*; Crist, *Cristatella mucedo*; Turb, Turbellaria; Daph, *Daphnia*; Ley, *Leydigia*; Ostra, Ostracoda; Bival, Bivalvia; Gastro, Gastropoda; Bith, *Bithynia tentaculata;* Lepto, *Leptocerus*; Athri, *Athripsodes*; Ortho, *Orthotrichia*; Pisces, Pisces; Pis.geo, *Piscicola geometra*; OM, organic matter; CARB, carbonates; MINER, mineral parts in the sediment

greater variability than in the K1 and K2 cores (Figure 5). The lack of linearity in many relationships between variables caused the OM/mineral matter curves to be non-significant. Nevertheless, this gradient was depicted and shaped axis 2, and the gradient along axis 1 was in line with the main clustering division. As stated earlier, of the three sediment variables, only CO_3^{2-} content was seen to have significant ($P < 0.03$) correlations with NMDS1 ($R = -0.76$) and NMDS2 ($R = 0.65$).

4 | DISCUSSION

4.1 | Climatic conditions preferred by *Lychnothamnus barbatus*

Analysis of data obtained from the meteorological station located ca. 20 km from Lake Kuźnickie indicated a significant increase in annual air temperature over the last 40 years, by more than 2°C

compared with the average temperature for the period 1951–1980 (Woś, 1994). In the same period, an increase in the annual precipitation was observed, which was considered typical for the temperate zone during global warming (Wentz et al., 2007). In addition, the average winter temperature for the period 1981–2010 increased by 1°C compared with the previous 30 years. Furthermore, the number of days with a temperature below 0°C decreased slightly (Woś, 1994). In general, the region followed a trend with warmer winters, which have recently been much more common in western Poland (Ustrnul et al., 2017).

Owing to the continuing climate change, alterations in the functioning of freshwater ecosystems are expected. While analysing climate change effects on *L. barbatus*, wide climatic plasticity must be considered. In Europe and North America, this species occurs mainly in a humid continental climate and a humid subtropical climate (Italy and the Balkans). In Asia, it has been reported from humid subtropical (Ling, Xie & Langangen, 2000) and humid tropical climates (Wang & Chou, 2006). In contrast, in Australia and Oceania (Casanova, García & Feist, 2003), it was noted in a semi-arid climate, a humid subtropical climate, and a tropical rainforest climate (Papua New Guinea).

In addition to wide climatic plasticity, a previous study of *L. barbatus* in Lake Kuźnickie showed that this species could adapt to warm winter conditions and overwinter in the form of a compact community (Pełechaty, Brzozowski & Pietruczuk, 2017). This may be illustrative of a competitive advantage of this species over that of annual hydromacrophytes, because overwintering charophyte meadows can effectively inhibit phytoplankton development despite the elevated concentration of nutrients observed after warm winters (Pełechata, Pełechaty & Pukacz, 2015).

4.2 | Palaeoenvironmental changes and evolution of aquatic vegetation

Despite the growing interest in the history of *Lychnothamnus* (Soulié-Märsche, 1989; Musacchio, 2010; Vicente, Csiki-Sava & Martín-Closas, 2019), its fossil record is known only from a few sites covering parts of the Holocene period. For instance, *Lychnothamnus* gyrogonites were found in palaeolacustrine sediments in the central Sahara (Petit-Maire & Riser, 1981), the Ganga Plain (India) sediments (Bhatia, 2006), and Lake Shkodra (Albania), where the disappearance of *L. barbatus* occurred approximately 1,300 cal. years BP. This may have been caused by marshland changing to lakes in response to increasing water levels (Mazzini et al., 2015). Therefore, the present study is one of a few reports on *L. barbatus* macrofossils in Holocene sediments. Most often, palaeolimnological studies are based on single-core analysis, where the sediment is taken from a pelagic site (Kowalewski, 2014). Palaeolimnological studies conducted in the phytolittoral areas are rare and limited to shallow lakes (Mazzini et al., 2015; Kornijów et al., 2016; Kowalewski et al., 2016). The advantage of the present study lies in the fact that it is based on three sediment cores collected along a depth gradient of the phytolittoral area. With this approach, changes can be described that occur in the Lake Kuźnickie phytolittoral area in time and space for the last millennium. Because of the differences in the age of collected sediments and different core collection depths, zones were distinguished and assigned to four temporal phases.

4.2.1 | Phase 1: Ca. AD 970–1050 to 1380–1480; subzone K3-1a

The oldest sediments were encountered only in core K3, taken from the area with the deepest water. The age of the core base was dated to approximately AD 1000 (Table 2), and the upper limit of this subzone, assuming a stable SAR of 0.03 cm year^{-1}, may be assessed at ca. AD 1380–1480 because of the lack of additional age control.

Moderate amounts of *Chara* spp. in samples from the lower part of this subzone may indicate the presence of a charophyte community, including trace amounts of *L. barbatus*, a new species for the lake, growing on the mineral bottom in transparent water. The indicators found in the upper part of the sediments suggested that this phase experienced an increase in water level, followed by a deterioration of the light conditions, resulting in a decline of macrophytes from the site. This might be related to the wet climatic phase characterized by high lake water levels recorded between approximately 1150 and 1350 years BP in Lake Strzeszyńskie in Poznań, located ca. 60 km to the north west of Lake Kuźnickie (Pleskot et al., 2018), as well as on a broader regional scale (Magny, 2004; Starkel et al., 2013).

4.2.2 | Phase 2: Ca. AD 1380–1480 to 1650–1750; subzones K3-1b, K3-2, and K1-1

In this phase, shallow phytolittoral vegetation was poorly developed (K1-1a). Proportions of the charophytes and vascular plants were small. At the deepest site (K3-1b), significant development of submerged vegetation was visible compared with phase 1. However, in this phase (K3-1b), the presence of *L. barbatus* is doubtful because few of its oospores were found. These could have been mixed downwards from the overlying sediment layers or transported from deeper sites. This period was characterized by the dominance of *Chara* sp., which corresponded to the Spörer minimum (Ogurtsov, 2019), one of the coldest periods during the Little Ice Age (O'Brien et al., 1995). *Potamogeton* sp. and *Ceratophyllum* sp. in sediments indicated an increase in water trophy. However, the dominance of *Chara* sp. indicates high water transparency and the maintenance of clear water status.

In the deeper core, K3-2, the number of oospores of *Chara* sp. decreased noticeably during the same period, whereas the abundance of *L. barbatus* was stable (K3-2), and the species competed strongly for habitats with other hydromacrophytes.

Vascular plants were common, although changeable through time, and their proportion increased compared with that in the previous zone.

4.2.3 | Phase 3: The 18th century to the first half of the 20th century; K1-2, K2-1, K2-2, and K3-3 (9–3 cm)

In the shallowest part of the phytolittoral (K1-2), the proportion of charophytes increased slightly compared with phase 2. An upward trend in the share of co-dominating *L. barbatus* and *Chara* sp. was observed in the K2-1 zone. The species structure indicated low trophy and high water transparency. In the K2-2 zone, there was an increasing proportion of charophytes compared with zone K2-1 and a visible occurrence of vascular plants. In the deepest part of the phytolittoral area, in the K3-3 zone (except for the two uppermost samples), the number of *Chara* sp. in relation to the previous phase decreased, whereas that of *L. barbatus* increased and dominated the vegetation structure of the deepest site. Because it occurred after the end of the Little Ice Age, the warming climate might be an important driving factor. Moreover, the lowering of the water level during this phase also had a positive impact on aquatic vegetation development because, in the second half of the 19th century, a drainage ditch was created, the formation of which was associated with the extraction of peat from the northern part of the Lake Kuźnickie catchment.

4.2.4 | Phase 4: Second half of the 20th century and the beginning of the 21st century; K1-3, K2-3, and K3-3 (two upper samples)

In this phase, the amount of OM increased significantly in each of the sediment cores, corresponding with the period of water quality deterioration in the second half of the 20th century. Anthropogenic eutrophication of Lake Kuźnickie and the introduction of herbivorous grass carp (Szyper et al., 1980) caused the disappearance of many species of hydromacrophytes, including *L. barbatus* (Pełechaty, Brzozowski & Pietruczuk, 2017). However, a constant proportion of oospores of *L. barbatus* was observed in this phase in all sediment cores. This contrasts with in-situ observations suggesting a significant decline in its abundance (Pełechaty, Brzozowski & Pietruczuk, 2017). Perhaps some individuals or small patches survived the period of nutrient enrichment and the effects of grass carp on the vegetation of the lake. The oospore bank deposited in lake sediments must have contributed to the recovery of the *L. barbatus* population in Lake Kuźnickie.

The sedimentary record documented a response of hydrobionts to the declining environmental conditions. An increased proportion of colonies of *Gloeotrichia* sp. and the highest abundance of zooplankton were recorded at the middle and deep phytolittoral areas, coinciding with a decrease in the number of *C. mucedo* and hydromacrophytes. In contrast, in the shallow phytolittoral core (K1-3), the proportion of *Gloeotrichia* sp. decreased, whereas charophytes, mainly *L. barbatus*, reached their maximum development. The rapid growth of phytoplankton probably decreased water transparency and reduced the presence of macrophytes in deeper littoral sites (cores K2 and K3). As a result, charophytes withdrew to shallower sites, where they successfully competed with other macrophytes and phytoplankton for resources. In contrast, seeds of vascular plants were also recorded in the upper part of the K1-3 zone; consequently, the dominance of *L. barbatus* at a shallow site was not complete, and an increase in water fertility promoted the development of taxa with a wide ecological range.

4.3 | Conservation and management of lakes with *Lychnothamnus barbatus*

Because *L. barbatus* is one of the rarest species of charophytes globally, representing the monotypic genus *Lychnothamnus*, the entire lineage is threatened with extinction. Owing to the small number of sites hosting this species (Pełechaty, Brzozowski & Pietruczuk, 2017), there is a need to identify the most critical conservation measures to prevent the degradation and loss of its habitats. The most stable and numerous habitats of *L. barbatus* are lakes, whereas ephemeral habitats, such as intermittent rivers (in Australia) and rice fields (in Bangladesh and Italy), are much more difficult to protect because of their instability. Therefore, the conservation measures proposed here are aimed at lacustrine populations of *L. barbatus* located mainly in Europe but are also potentially applicable in North America.

Significant possibilities for protecting lakes with *L. barbatus* populations in Europe have been created by EU legislation. According to the EU Habitats Directive (Council of the European Communities, 1992) EU Member States should designate high-quality sites containing the habitats listed in Annex I as Special Areas of Conservation (SACs). Together, SACs contribute to the Natura 2000 network around Europe. Lakes with charophyte vegetation are included in Annex I as the habitat 3140: 'Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp'. Lake Kuźnickie is a unique lake that meets the criteria of this habitat type because of the occurrence of extensive charophyte vegetation, including the dominant species *L. barbatus*. Unfortunately, however, it has not been selected as an SAC, and therefore it is not covered by this form of protection. The nearest Natura 2000 site, PLH300028 'Barłożnia Wolsztyńska', is located approximately 5 km from Lake Kuźnickie and mostly covers a mosaic of wetland habitats. We suggest that this area should be extended to include this lake, representing habitat 3140. Moreover, to maintain the appropriate ecological status of lakes with *L. barbatus*, it is advisable to monitor these valuable ecosystems regularly, in line with the provisions of the EU Water Framework Directive (Council of the European Communities, 2000). Lake Kuźnickie is included in the State Environmental Monitoring and is monitored by the Voivodeship Inspectorate for Environmental Protection in Poznań (Pełechaty, Brzozowski & Pietruczuk, 2017).

An essential aspect of protecting the *L. barbatus* population is the reduction of nutrient loads from the catchment area. Analysis of the land cover of the Lake Kuźnickie catchment did not show any significant changes over the last 120 years. In addition, for each of the periods analysed (Table 1), forests covered more than 90% of the catchment area. In lakes of Central Europe with abundant *L. barbatus* sites, catchments are characterized by a high proportion of forests along the shorelines (Kolada, 2009; Pełechaty et al., 2009; Sinkevičienė, 2010), which have a protective function against eutrophication because they serve as a natural barrier for nutrients (Hazlett et al., 2008; Sender et al., 2016).

Another critical factor for conservation of *L. barbatus* is sustainable fishing management, expressed by strict stock control in line with the type of fishing undertaken in the lakes. The proportion of predatory fish species should be increased compared with that of cyprinids, and a prohibition on introducing alien fish species should be enforced. It is also essential to counteract the removal of charophytes from the shallow-water zone, often to allow footbridge construction by anglers. Furthermore, it is unacceptable to use excessive amounts of ground bait for fish in regions overgrown by charophyte vegetation. The last two of these impacts contribute to eliminating shallow-water sites of *L. barbatus*, which are more prone to disappearance because of high instability caused by water level fluctuations exacerbated by global warming. It must be emphasized that protecting the entire gene pool of *L. barbatus* is crucial. This mainly concerns the shallow-water ecotypes, which, although morphologically more plastic, produce fewer oospores (Brzozowski & Pełechaty, 2020); thus, their chances of survival in the sediment oospore bank decrease. The importance of analysing charophyte oospores and angiosperm macroremains, applied in palaeolimnological studies, is underestimated in contributing to the protection of aquatic vegetation. This type of study enables the reconstruction of the responses of plant communities to environmental changes occurring in the past and, consequently, helps to predict the future dynamics of macrophytes in freshwater ecosystems undergoing change.

In the study reported here, the composition of past vegetation was interpreted from the proportion of diaspores (oospores, seeds, bulbils, tubers, and vegetative parts of macrophytes) buried in the sediment. In the top layers of sediment, diaspores were over-represented compared with the deeper sediments (Grillas et al., 1993). Many charophyte species produce numerous oospores that, because of a low germination rate, are adapted to long-term survival in a dormant state; thus, in deeper sediments, they may accumulate in high numbers compared with less persistent bulbils and angiosperm macroremains (Van den Berg, Coops & Simons, 2001; Bonis & Grillas, 2002; Schubert et al., 2018). In contrast to the short-lived hibernacles of vascular plants, oospores serve as long-term diaspore banks (Casanova & Brock, 1996; Van den Berg, Coops & Simons, 2001; Bonis & Grillas, 2002), which in palaeoreconstructions help to determine charophyte dominance in the past vegetation. This is because the density of oospores in the sediments is positively correlated with the charophyte cover (Van den Berg, Coops & Simons, 2001). However, the absence of oospores does not necessarily indicate the absence of charophyte communities in the submerged vegetation. It may result from the fact that charophytes present in the past reproduced vegetatively (Skurzyński & Bociąg, 2011); for example, only individuals of one sex of dioecious species were present (Larkin et al., 2018). Therefore, conclusions based on vegetation composition in the past using the frequency of diaspores in the sediments should be drawn carefully. However, the bank of diaspores deposited in the sediment provides a valuable archive of the composition and vegetation changes over time. Nevertheless, to avoid over- or under-interpretation, additional proxies should be used to validate the conclusions drawn from the analysis of plant macroremains. *C. mucedo* statobasts were used as a proxy that suggested well-developed charophyte vegetation in the present study.

In the era of water quality decline, ecological education of local communities emerges as an elementary aspect in the protection of *Chara* lakes. Training for children, seminars, and citizen science may increase ecological awareness regarding the positive impact of submerged aquatic vegetation on water quality and its recreational attractiveness. From the perspective of the protection of the *L. barbatus* population, it would be beneficial to create educational display boards near beaches and other tourist facilities, instructing the public regarding the rarity of this macroalga and the benefits of its occurrence in water bodies.

In summary, the oospore bank of *L. barbatus* deposited in the bottom sediment allowed recovery of this species after its decline in the period of water quality deterioration in the second half of the 20th century. The contemporary renewal of *L. barbatus*, coinciding with global warming, seems to be reflected in a sharp increase in the population of *L. barbatus* at the end of the Little Ice Age. This study highlights the importance of palaeolimnological research for understanding the response of contemporary vegetation to changes in environmental conditions. This is particularly important for establishing effective conservation measures in aquatic environments influenced by climate change.

ACKNOWLEDGEMENTS

The study was financed by the Polish Ministry of Science and Higher Education as project no. DI2015017045 'Recovery of the population of an endangered charophyte species, *Lychnothamnus barbatus* in light of climate change'. According to Polish law in species protection, samples of the species studied were collected based on a permit obtained from the Regional Directorate for Environmental Protection in Poznań (no. WPN-II.6400.5.2016.WC.2). Public data from the meteorological station of the Institute of Meteorology and Water Management (Wielichowo, station code 252160230) were used and processed in the study. We are grateful to two reviewers and the Editor for their valuable remarks and comments that helped to improve the manuscript. The cost of open access was covered thanks to the financial support received by the authors (Application no. 011/08/POB1/0020) from the Initiative of Excellence - Research

University (05/IDUB/2019/94) at Adam Mickiewicz University, Poznań, Poland.

CONFLICT OF INTEREST

No conflict of interest has been declared by the authors.

DATA ACCESSIBILITY

The materials analysed were archived in the Department of Hydrobiology, Adam Mickiewicz University in Poznań. Data have not been published in public repositories.

AUTHOR CONTRIBUTIONS

MB and MP were responsible for the conceptualization of this research. MB, GK, WS, and MP performed the formal analysis, with support from LK. MB, GK, WS, and MP were involved in the investigation and methodology, with support from LK; MP, MB, GK, and WS were involved in visualization, with support from LK. MB was responsible for funding acquisition, project administration, and resources. MP supervised the project. MB wrote the original draft, with support from GK, WS, and MP. Review and editing of the draft was performed by MB and MP, with support from GK and WS.

ORCID

Michał Brzozowski https://orcid.org/0000-0002-8028-2129
Grzegorz Kowalewski https://orcid.org/0000-0001-9668-1071
Witold Szczuciński https://orcid.org/0000-0003-2466-2263
Lech Kaczmarek https://orcid.org/0000-0002-5817-5976
Mariusz Pełechaty https://orcid.org/0000-0002-4075-6561

REFERENCES

Auderset Joye, D. & Rey-Boissezon, A. (2015). Will charophyte species increase or decrease their distribution in a changing climate? *Aquatic Botany*, 120(A), 73–83. https://doi.org/10.1016/j.aquabot.2014.05.003

Bartosiewicz, M., Ptak, M., Woolway, R.I. & Sojka, M. (2020). On thinning ice: Effects of atmospheric warming, changes in wind speed and rainfall on ice conditions in temperate lakes (northern Poland). *Journal of Hydrology*, 597, 125724. https://doi.org/10.1016/j.jhydrol.2020.125724

Beilby, M.J. & Casanova, M.T. (2014). *The physiology of characean cells*. Berlin, Germany: Springer.

Bennett, K.D. (1996). Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, 132(1), 155–170. https://doi.org/10.1111/j.1469-8137.1996.tb04521.x

Bhatia, S.B. (2006). Ecological parameters and dispersal routes of *Lychnothamnus barbatus* (Characeae) in the Early–Middle Holocene from the Ganga Plain, India. *Cryptogamie Algologie*, 27(4), 341–356.

Birks, H.J.B. (2014). Challenges in the presentation and analysis of plant-macrofossil stratigraphical data. *Vegetation History and Archaeobotany*, 23, 309–330. https://doi.org/10.1007/s00334-013-0430-2

Blaženčić, J., Stevanović, B., Blaženčić, Ž. & Stevanović, V. (2006). Red data list of charophytes in the Balkans. *Biodiversity and Conservation*, 15, 3445–3457. https://doi.org/10.1007/s10531-005-2008-5

Blindow, I. (1988). Phosphorus toxicity in *Chara*. *Aquatic Botany*, 32(4), 393–395. https://doi.org/10.1016/0304-3770(88)90110-6

Blindow, I. (1992). Decline of charophytes during eutrophication: Comparison with angiosperms. *Freshwater Biology*, 28(1), 9–14. https://doi.org/10.1111/j.1365-2427.1992.tb00557.x

Blindow, I., Hargeby, A. & Hilt, S. (2014). Facilitation of clear-water conditions in shallow lakes by macrophytes: Differences between charophyte and angiosperm dominance. *Hydrobiologia*, 737, 99–110. https://doi.org/10.1007/s10750-013-1687-2

Bonis, A. & Grillas, P. (2002). Deposition, germination and spatio-temporal patterns of charophyte propagule banks: A review. *Aquatic Botany*, 72(3–4), 235–248. https://doi.org/10.1016/S0304-3770(01)00203-0

Bostock, P.D. & Holland, A.E. (Eds.) (2010). *Census of the Queensland flora: 2010*. Brisbane, QLD, Australia: Queensland Herbarium, Biodiversity and Ecosystem Sciences, Department of Environment and Resource Management.

Bronk Ramsey, C. (2009). Bayesian analysis of radiocarbon dates. *Radiocarbon*, 51(1), 337–360. https://doi.org/10.1017/S0033822200033865

Brzozowski, M., Palomares Cabanilles, M., Kowalewski, G. & Pełechaty, M. (2019). Environmental factors responsible for the gyrogonite formation by an endangered macroalga, *Lychnothamnus barbatus*, a fertility indicator of past and present lacustrine ecosystems. *Limnologica*, 77, 125686. https://doi.org/10.1016/j.limno.2019.125686

Brzozowski, M., Pełechata, A., Kaczmarek, L. & Pełechaty, M. (2021). Transformation and simplification of aquatic vegetation structure and reoligotrophication of a lake during the last 40 years. *Acta Societatis Botanicorum Poloniae*, 90, 905. https://doi.org/10.5586/asbp.905

Brzozowski, M. & Pełechaty, M. (2020). Broad morphological and reproductive variability of the endangered macroalga *Lychnothamnus barbatus* in the depth gradient. *Aquatic Botany*, 165, 103239. https://doi.org/10.1016/j.aquabot.2020.103239

Brzozowski, M., Pełechaty, M. & Pietruczuk, K. (2018). Co-occurrence of the charophyte *Lychnothamnus barbatus* with higher trophy submerged macrophyte indicators. *Aquatic Botany*, 151, 51–55. https://doi.org/10.1016/j.aquabot.2018.08.003

Casanova, M.T. & Brock, M.A. (1996). Can oospore germination patterns explain charophyte distribution in permanent and temporary wetlands? *Aquatic Botany*, 54(4), 297–312. https://doi.org/10.1016/0304-3770(96)01032-7

Casanova, M.T., García, A. & Feist, M. (2003). The ecology and conservation of *Lychnothamnus barbatus* (Characeae). *Acta Microbiologica Sinica*, 20(2), 118–128.

Choiński, A., Ptak, M., Skowron, R. & Strzelczak, A. (2015). Changes in ice phenology on Polish lakes from 1961 to 2010 related to location and morphometry. *Limnologica*, 53, 42–49. https://doi.org/10.1016/j.limno.2015.05.005

Choudhury, M.I., Urrutia-Cordero, P., Zhang, H., Ekvall, M.K., Medeiros, L.R. & Hansson, L.A. (2019). Charophytes collapse beyond a critical warming and brownification threshold in shallow lake systems. *Science of the Total Environment*, 661, 148–154. https://doi.org/10.1016/j.scitotenv.2019.01.177

Council of the European Communities. (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities*, L206, 7–50.

Council of the European Communities. (2000). Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities*, L327, 1–73.

Czernecki, B. & Ptak, M. (2018). The impact of global warming on lake surface water temperature in Poland — The application of empirical–statistical downscaling, 1971–2100. *Journal of Limnology*, 77(2), 330–348. https://doi.org/10.4081/jlimnol.2018.1707

Dziuba, M.K., Herdegen-Radwan, M., Pluta, E., Wejnerowski, Ł., Szczuciński, W. & Cerbin, S. (2020). Temperature increase altered *Daphnia* community structure in artificially heated lakes: A potential scenario for a warmer future. *Scientific Reports*, 10, 13956. https://doi.org/10.1038/s41598-020-70294-6

Gołdyn, R. (1983). Zbiorowiska roślinności zanurzonej jeziora Dominickiego i jeziora Kuźnickiego na Pojezierzu Wielkopolskim [Submerged plant communities of the Dominickie Lake and the Kuźnickie Lake in Wielkopolska Lakeland]. *Badania Fizjograficzne NAD Polską Zachodnią, Seria B – Botanika*, 34, 165–192.

Grillas, P., Garcia-Murillo, P., Geertz-Hansen, O., Marbà, N., Montes, C., Duarte, C.M. et al. (1993). Submerged macrophyte seed bank in a Mediterranean temporary marsh: Abundance and relationship with established vegetation. *Oecologia*, 94, 1–6. https://doi.org/10.1007/BF00317293

Grimm, E.C. (1987). CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences*, 13(1), 13–35. https://doi.org/10.1016/0098-3004(87)90022-7

Hazlett, P., Broad, K., Gordon, A., Sibley, P., Buttle, J. & Larmer, D. (2008). The importance of catchment slope to soil water N and C concentrations in riparian zones: Implications for riparian buffer width. *Canadian Journal of Forest Research*, 38(1), 16–30. https://doi.org/10.1139/X07-146

Heiri, O., Lotter, A.F. & Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. *Journal of Paleolimnology*, 25, 101–110. https://doi.org/10.1023/A:1008119611481

Intergovernmental Panel on Climate Change. (2013). *Climate Change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Juggins, S. (2017). *rioja: Analysis of Quaternary science data*. Available at: http://cran.r-project.org/package=rioja

Karol, K.G., Skawinski, P.M., McCourt, R.M., Nault, M.E., Evans, R., Barton, M.E. et al. (2017). First discovery of the charophycean green alga *Lychnothamnus barbatus* (Charophyceae) extant in the New World. *American Journal of Botany*, 104(7), 1108–1116. https://doi.org/10.3732/ajb.1700172

Kolada, A. (2009). Is the *Lychnothamnus barbatus* (Meyen) Leonhardi 1963 a good indicator of water quality? A new location of the species in Gorskie Lake near Gostynin (central Poland). *Oceanological and Hydrobiological Studies*, 38(2), 39–43.

Kornijów, R., Kowalewski, G., Sugier, P., Kaczorowska, A., Gąsiorowski, M. & Woszczyk, M. (2016). Towards a more precisely defined macrophyte-dominated regime: The recent history of a shallow lake in eastern Poland. *Hydrobiologia*, 772, 45–62. https://doi.org/10.1007/s10750-015-2624-3

Kowalewski, G. (2014). Alogeniczne I autogeniczne składowe zarastania jezior: Hipoteza wahań poziomu wody [Allogenic and autogenic components of lake overgrowth: Hypothesis of water level fluctuations]. *Studia Limnologica et Telmatologica*, *Monographiae I*. Poznań, Poland: Bogucki Wydawnictwo Naukowe.

Kowalewski, G.A., Kornijów, R., McGowan, S., Kaczorowska, A., Bałaga, K., Namiotko, T. et al. (2016). Disentangling natural and anthropogenic drivers of changes in a shallow lake using palaeolimnology and historical archives. *Hydrobiologia*, 767, 301–320. https://doi.org/10.1007/s10750-015-2510-z

Kruskal, J.B. (1964). Nonmetric multidimensional scaling: A numerical method. *Psychometrika*, 29, 115–129. https://doi.org/10.1007/BF02289694

Larkin, D.J., Monfils, A.K., Boissezon, A., Sleith, R.S., Skawinski, P.M., Welling, C.H. et al. (2018). Biology, ecology, and management of starry stonewort (*Nitellopsis obtusa*; Characeae): A Red-listed Eurasian green alga invasive in North America. *Aquatic Botany*, 148, 15–24. https://doi.org/10.1016/j.aquabot.2018.04.003

Legendre, P. & Legendre, L.F.J. (1998). *Numerical ecology*, 2nd English edition. Amsterdam, Netherlands: Elsevier.

Ling, Y.J., Xie, S.L. & Langangen, A. (2000). Charales of China. *Nova Hedwigia*, 71(1–2), 69–94.

Magny, M. (2004). Holocene climate variability as reflected by mid-European lake-level fluctuations and its probable impact on prehistoric human settlements. *Quaternary International*, 113(1), 65–79. https://doi.org/10.1016/S1040-6182(03)00080-6

Martín-Closas, C., Wójcicki, J.J. & Fonollá, L. (2006). Fossil charophytes and hydrophytic angiosperms as indicators of lacustrine trophic change. A case study in the Miocene of Catalonia (Spain). *Cryptogamie Algologie*, 27(4), 357–379.

Mazzini, I., Gliozzi, E., Koci, R., Soulie-Märsche, I., Zanchetta, G., Baneschi, I. et al. (2015). Historical evolution and Middle to Late Holocene environmental changes in Lake Shkodra (Albania): New evidences from micropaleontological analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 419, 47–59. https://doi.org/10.1016/j.palaeo.2014.08.012

McKee, B.A., Nittrouer, C.A. & DeMaster, D.J. (1983). Concepts of sediment deposition and accumulation applied to the continental shelf near the mouth of the Yangtze River. *Geology*, 11(11), 631–633. https://doi.org/10.1130/0091-7613(1983)11<631:COSDAA>2.0.CO;2

Mirek, Z., Zarzycki, K., Wojewoda, W. & Szeląg, Z. (Eds.) (2006). *Red list of plants and fungi in Poland*. Kraków, Poland: W Szafer Institute of Botany, Polish Academy of Sciences.

Moss, B., Hering, D., Green, A.J., Aidoud, A., Becares, E., Beklioglu, M. et al. (2009). Climate change and the future of freshwater biodiversity in Europe: A primer for policy-makers. *Freshwater Reviews*, 2(2), 103–130. https://doi.org/10.1608/FRJ-2.2.1

Musacchio, E.A. (2010). Upper Cretaceous *Lychnothamnus*, *Nitella*, and *Tolypella* (Charophyta) from Zampal, Argentina. *Cretaceous Research*, 31(5), 461–472. https://doi.org/10.1016/j.cretres.2010.05.010

O'Brien, S.R., Mayewski, P.A., Meeker, L.D., Meese, D.A., Twickler, M.S. & Whitlow, S.I. (1995). Complexity of Holocene climate reconstructed from a Greenland ice core. *Science*, 270(5244), 1962–1964. https://doi.org/10.1126/science.270.5244.1962

Ogurtsov, M.G. (2019). The Spörer minimum was deep. *Advances in Space Research*, 64(5), 1112–1116. https://doi.org/10.1016/j.asr.2019.06.011

Oksanen, J. (2010). Multivariate analysis of ecological communities in R: vegan tutorial v. 1.17-12. Available at: http://phylodiversity.net/azanne/csfar/images/8/85/Vegan.pdf

Pełechata, A., Pełechaty, M. & Pukacz, A. (2015). Winter temperature and shifts in phytoplankton assemblages in a small *Chara*-lake. *Aquatic Botany*, 124, 10–18. https://doi.org/10.1016/j.aquabot.2015.03.001

Pełechaty, M., Brzozowski, M. & Pietruczuk, K. (2017). Overwintering and gyrogonite formation by the rare and endangered indicative macroalga *Lychnothamnus barbatus* (Meyen) Leonh. in eutrophic conditions. *Aquatic Botany*, 139, 19–24. https://doi.org/10.1016/j.aquabot.2017.02.005

Pełechaty, M., Gąbka, M., Sugier, P., Pukacz, A., Chmiel, S., Ciecierska, H. et al. (2009). *Lychnothamnus barbatus* in Poland: Habitats and associations. *Charophytes*, 2(1), 13–18.

Pełechaty, M., Pronin, E. & Pukacz, A. (2014). Charophyte occurrence in *Ceratophyllum demersum* stands. *Hydrobiologia*, 737, 111–120. https://doi.org/10.1007/s10750-013-1622-6

Petit-Maire, N. & Riser, J. (1981). Holocene lake deposits and palaeoenvironments in Central Sahara, northeastern Mali. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 35, 45–61. https://doi.org/10.1016/0031-0182(81)90093-6

Pleskot, K., Tjallingii, R., Makohonienko, M., Nowaczyk, N. & Szczuciński, W. (2018). Holocene paleohydrological reconstruction of Lake Strzeszyńskie (western Poland) and its implications for the central European climatic transition zone. *Journal of Paleolimnology*, 59, 443–459. https://doi.org/10.1007/s10933-017-9999-2

Puche, E., Sánchez-Carrillo, S., Álvarez-Cobelas, M., Pukacz, A., Rodrigo, M.A. & Rojo, C. (2018). Effects of overabundant nitrate and

warmer temperatures on charophytes: The roles of plasticity and local adaptation. *Aquatic Botany*, 146, 15–22. https://doi.org/10.1016/j.aquabot.2018.01.003

Raabe, U., Pukacz, A., Peschel, T. & Müller, R. (2012). Die Bart-Glantzleuchteralge, *Lychnothamnus barbatus* (Meyen) Leonh., in Deutschland wieder aufgefunden. *Verhandlungen des Botanischen Vereins von Berlin und Brandenburg*, 145, 235–248.

Radziej, J. (1959). Jezioro Kuźnickie — Mapa batymetryczna [Lake Kuźnickie — Bathymetric map]. Instytut Rybactwa Śródlądowego WSR Olsztyn.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B. et al. (2013). IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, 55(4), 1869–1887. https://doi.org/10.2458/azu_js_rc.55.16947

Richter, D. & Gross, E.M. (2013). *Chara* can outcompete *Myriophyllum* under a low phosphorus supply. *Aquatic Sciences*, 75, 457–467. https://doi.org/10.1007/s00027-013-0292-9

Robbins, J.A. & Edgington, D.N. (1975). Determination of recent sedimentation rates in Lake Michigan using Pb-210 and Cs-137. *Geochimica et Cosmochimica Acta*, 39(3), 285–304. https://doi.org/10.1016/0016-7037(75)90198-2

Rodrigo, M.A., Alonso-Guillén, J.L. & Soulié-Märsche, I. (2010). Reconstruction of the former charophyte community out of the fructifications identified in Albufera de Valencia lagoon sediments. *Aquatic Botany*, 92(1), 14–22. https://doi.org/10.1016/j.aquabot.2009.09.002

Rojo, C., Carramiñana, M., Cócera, D., Roberts, G.P., Puche, E., Calero, S. et al. (2017). Different responses of coexisting *Chara* species to foreseeable Mediterranean temperature and salinity increases. *Aquatic Botany*, 138, 53–63. https://doi.org/10.1016/j.aquabot.2017.01.003

Schnittler, M. & Ludwig, G. (1996). Zur Methodik der Erstellung Roter Listen [On the methodology of creating Red Lists]. In: G. Ludwig, M. Schnittler (Eds.) *Rote Liste gefährdeter Pflanzen Deutschlands*, Schriftenreihe für Vegetationskunde Heft 28. Münster, Germany: Landwirtschaftsverlag, pp. 709–739.

Schubert, H., Blindow, I., Bueno, N.C., Casanova, M.T., Pełechaty, M. & Pukacz, A. (2018). Ecology of charophytes — Permanent pioneers and ecosystem engineers. *Perspectives in Phycology*, 5(1), 61–74. https://doi.org/10.1127/pip/2018/0080

Sender, J., Maślanko, W., Rózańska-Boczula, M. & Garbowski, M. (2016). Floristic diversity of midforest lakes (Sobibór Landscape Park, Poland). *Ekologia Bratislava*, 35(4), 359–370. https://doi.org/10.1515/eko-2016-0029

Siemińska, J., Bąk, M., Dziedzic, J., Gąbka, M., Gregorowicz, P., Mrozińska, T. et al. (2006). Red List of the algae in Poland. In: Z. Mirek, K. Zarzycki, W. Wojewoda, Z. Szeląg (Eds.) *Red List of plants and fungi in Poland*. Kraków, Poland: W Szafer Institute of Botany, Polish Academy of Sciences, pp. 35–52.

Sinkevičienė, Z. (2010). Morphological variation in *Lychnothamnus barbatus* (Meyen) Leonh. in Lake Balsys (Lithuania). *Charophytes*, 2(1), 25–30.

Sinkevičienė, Z. & Urbaitė-Maževič, N. (2012). *Lychnothamnus barbatus* (Meyen) Leonh.—Rediscovered in shallow Lake Šventininkai (Lithuania) after 50 years. *Biodiversity: Research and Conservation*, 25, 91–96. https://doi.org/10.2478/v10119-012-0012-7

Skurzyński, P. & Bociąg, K. (2011). Vegetative propagation of *Chara rudis* (Characeae, Chlorophyta). *Phycologia*, 50(2), 194–201. https://doi.org/10.2216/09-64.1

Sleith, R.S., Wehr, J.D. & Karol, K.G. (2018). Untangling climate and water chemistry to predict changes in freshwater macrophyte distributions. *Ecology and Evolution*, 8(5), 2802–2811. https://doi.org/10.1002/ece3.3847

Soulié-Märsche, I. (1989). *Étude comparée de gyrogonites de charophytes actuelles et fossiles et phylogénie des genres actuels [Comparative study of the gyrogonites of living and fossil charophytes and phylogeny of the extant genera]*. Millau, France: Imprimerie des Tilleuls.

Soulié-Märsche, I. & García, A. (2015). Gyrogonites and oospores, complementary viewpoints to improve the study of the charophytes (Charales). *Aquatic Botany*, 120(A), 7–17. https://doi.org/10.1016/j.aquabot.2014.06.003

Starkel, L., Michczyńska, D., Krąpiec, M., Margielewski, W., Nalepka, D. & Pazdur, A. (2013). Progress in the Holocene chrono-climatostratigraphy of Polish territory. *Geochronometria*, 40(1), 1–21. https://doi.org/10.2478/s13386-012-0024-2

Stewart, N. & Church, J.M. (1992). *Red data books of Britain & Ireland: Stoneworts*. Peterborough, UK: Joint Nature Conservation Committee.

Sugier, P., Pełechaty, M., Gąbka, M., Owsianny, P.M., Pukacz, A., Ciecierska, H. et al. (2010). *Lychnothamnus barbatus*: Global history and distribution in Poland. *Charophytes*, 2(1), 19–24.

Szyper, H., Romanowicz, W., Stempniak, M., Gołdyn, R., Jankowski, A. & Lubner, H. (1980). Wpływ zanieczyszczeń z terenów rekreacyjnych na stan czystości wybranych jezior [Impact of pollution from recreational areas on the water quality of selected lakes]. Instytut Kształtow, Środowiska Oddział w Poznaniu, manuscript.

Urbaniak, J. & Gabka, M. (2014). *Polish charophytes. An illustrated guide to identification*. Wrocław, Poland: Wroclaw University of Environmental and Life Sciences.

Ustrnul, Z., Limanówka, M., Biernacik, D., Czekierda, D. & Pryc, R. (2017). Climate Monitoring Bulletin: Winter 2016/2017 (December 2016–February 2017). Institute of Meteorology and Water Management, Warsaw. Available at: http://klimat.imgw.pl/pl/biuletyn-monitoring/#2017/zima

Van den Berg, M.S., Coops, H. & Simons, J. (2001). Propagule bank buildup of *Chara aspera* and its significance for colonization of a shallow lake. *Hydrobiologia*, 462, 9–17. https://doi.org/10.1023/A:1013125603555

Van den Berg, M.S., Scheffer, M., Van Nes, E. & Coops, H. (1999). Dynamics and stability of *Chara* sp. and *Potamogeton pectinatus*. *Hydrobiologia*, 408, 335–342. https://doi.org/10.1023/A:1017074211970

Vicente, A., Csiki-Sava, Z. & Martín-Closas, C. (2019). European charophyte evolution across the Cretaceous–Paleogene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 533, 109244. https://doi.org/10.1016/j.palaeo.2019.109244

Wang, W.-L. & Chou, J.-Y. (2006). Biogeography of *Lychnothamnus barbatus* (Charophyta): Molecular and morphological comparisons with emphasis on a newly discovered population from Taiwan. *Cryptogamie Algologie*, 27(4), 461–471.

Wentz, F.J., Ricciardulli, L., Hilburn, K. & Mears, C. (2007). How much more rain will global warming bring? *Science*, 317(5835), 233–235. https://doi.org/10.1126/science.1140746

Woś, A. (1994). *Klimat niziny wielkopolskiej [The climate of the Wielkopolska lowland]*. Poznań, Poland: Wydawnictwo Naukowe UAM.

How to cite this article: Brzozowski, M., Kowalewski, G., Szczuciński, W., Kaczmarek, L. & Pełechaty, M. (2021). Preliminary evidence of an endangered species benefiting from moderate climate warming: A palaeolimnological study of the charophyte *Lychnothamnus barbatus*. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(10), 2673–2689. https://doi.org/10.1002/aqc.3672